REPRODUCTIVE AND GENETIC VARIATION AMONG CARIBBEAN GORGONIANS: THE DIFFERENTIATION OF *PLEXAURA KUNA*, NEW SPECIES

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ABSTRACT

Ecophenotypic variation is common among many coral reef benthic invertebrates. However, there is no consensus on whether this variation is generated by genetically diverse and phenotypically plastic species or whether it is indicative of a more species-rich fauna than previously believed. Caribbean gorgonian species exhibit extensive variation in their sclerites and based on the variation among populations in the genus *Plexaura*, we describe *P. kuna*, new species. The sclerites of *P. kuna* are most similar to those of *Plexaura homomalla* but differ both qualitatively and quantitatively from those of *P. homomalla* and other congeners. Analysis of randomly amplified polymorphic DNA (RAPDs) indicates that *P. kuna* has alleles that are absent in both *Plexaura homomalla* and *Plexaura homomalla* forma *kükenthali*. The reproductive cycle of *P. kuna* in Panama differs from that of *P. homomalla* and there is only limited opportunity for hybridization between the two species. Genetic and reproductive data can serve as important adjuncts in establishing the existence of species-level differences between morphologically distinct populations.

The increasing interest in biodiversity among both the scientific and lay community has focused attention on the incompleteness of our knowledge of even well studied floras and faunas. These difficulties are not surprising to invertebrate zoologists who often must identify taxa whose systematics are poorly known, and whose identification relies on morphologic features that are not readily observed. Among clonal organisms these difficulties are further exacerbated by what has generally been regarded as extensive phenotypic plasticity within species (Wijsman-Best, 1974; Veron and Pichon, 1976; Brakel, 1977; Foster, 1980).

Although there has been extensive interest in phenotypic and genetic variation among reef taxa, there has been a tendency to ignore the systematic repercussions of studies that demonstrate phenotypic and/or genotypic variation within taxa. Knowlton et al. (1992) have identified a clear example of such variation in the reef coral *Montastrea annularis*. The wide range of variation that they comment on has been known for decades (Graus and MacIntyre, 1976), but Knowlton et al. (1992) are the first in recent years to suggest that *M. annularis* is a complex of at least three species. Knowlton et al. (1992) based their conclusions on a combination of morphologic and genetic data. Imprecision in defining species such as *M. annularis,* can produce the incorrect interpretation of species' habitat range and specificity, overestimation of population size and physiologic tolerances, and among readily fossilized taxa the incorrect interpretation of ancient environments (Knowlton and Jackson, 1994). These potential errors have consequences for our development of ecological and evolutionary theory, management decisions and our understanding of global climate change.

Despite the call to arms issued by Knowlton and Jackson (1994), identifying taxa even in the presence of strong morphologic and genetic data is not clear cut. Indeed the status of *Montastrea annularis,* the case that led Knowlton et al. (1992) to their conclusions, has not been universally accepted as a species level difference (VanVeghel and Bak, 1993). The difficulty in assigning different morphotypes to different species in this case as in other studies, is deciding the level of phenotypic difference that corresponds to reproductive isolation. Although the identification

of species is based on phenotypic traits, the biologic species concept is based on reproductive isolation. The relationship between these traits is implicit in all taxonomic work, but the relationship between degrees of phenotypic variation and reproductive isolation are often unverified. In this paper we present a case in which genetic and reproductive data can be used to supplement data on morphologic differences among Caribbean gorgonians in the genus *Plexaura.* We do not argue that every species description must rely on genetic and reproductive data, but such information can provide an important adjunct to such efforts.

Caribbean coral reefs are in many places visually dominated by gorgonian corals. Among the most common Caribbean corals are those in the genus *Plexaura.* There are three recognized species of *Plexaura,* and two of these, *P. homomalla* and *P. flexuosa,* are found in a diverse array of habitats and sites (Lasker and Coffroth, 1983; Yoshioka and Yoshioka, 1989). The systematics of *Plexaura,* like all gorgonians, is based almost entirely on the types and sizes of the calcium carbonate sclerites that are embedded in the tissue of the colony.

The explosion of SCUBA based research that has occurred since 1961 has led to the collection of large numbers of specimens that do not readily fit the *Plexaura* species recognized by Bayer in his 1961 revision of the Caribbean plexaurids (F. M. Bayer, pers. comm.). Among these problematic groups are specimens from a *Plexaura* sp. population in Panama that one of us (HRL) first started working with in 1982. That work has produced a number of papers describing the ecology of this putative species, designated as *Plexaura* A in Lasker (1984). There are now reports on the taxon's reproductive biology (Brazeau and Lasker 1989), vegetative propagation (Lasker, 1984; Coffroth et al. 1992), ecology and population dynamics (Lasker, 1990, 1992) and colony form (Brazeau and Lasker, 1988). The characterization of *Plexaura* A as a distinct entity has also been important in analyses of grazing and browsing on gorgonians (Lasker, 1985; Lasker and Coffroth, 1988; Lasker et al., 1988; Vreeland and Lasker, 1989). Central to all of these studies has been the presumption that this *Plexaura* is a distinct species. As first discussed in Lasker (1984), *Plexaura* A has sclerites that differ from *Plexaura homomalla* and other *Plexaura* species, but those differences were never fully quantified.

Plexaura A and *Plexaura homomalla* are among the most studied of the Caribbean gorgonians, and it is essential to understand whether these morphotypes are separate species with many fixed genetic differences or whether they are genotypic and phenotypic variants all occurring in a single highly polymorphic species. The difficulties in establishing the taxonomic status of these *Plexaura* populations are illustrative of the problems in establishing the systematics of a wide range of reef invertebrates. In this paper we provide a name and description for *Plexaura* A and use genetic and reproductive differences to further demonstrate the reproductive isolation of this species.

METHODS

Sclerite Preparations.—Plexaura spp. were collected from the San Blas Islands, Panama; St. Croix, U.S. Virgin Islands; the Florida Keys and the Bahamas (Table 1). Samples were initially divided into three groups based on their gross morphologic appearance, *Plexaura* A, *Plexaura homomalla* forma *homomalla* (hereafter referred to as *P. homomalla*) and *Plexaura homomalla* forma *kükenthali.* Sclerites from rind, cortex and axial sheath were dissolved from the tissue using a 5% hypochlorite solution, examined and measured at 100×. Samples from branch tips, mid-colony and colony base were examined. The types of sclerites observed, range of sizes and degree of sculpturing were noted. Scanning electron micrographs were prepared using a Hitachi S800.

Table 1. Spindle morphology in *Plexaura kuna* and *Plexaura homomalla*. Mean (and standard deviation) was determined for 35 spindles from a single colony from each site. Species means are based on pooled data.

Species and collection site	Length (μm)	Width (μm)	L/W
Plexaura kuna, new species			
San Blas, Panama (type)	220.8 (52.7)	50.4 (20.5)	4.8 (1.3)
Exumas, Bahamas	269.7 (59.5)	45.9 (12.2)	6.1 (1.6)
Chub Cay, Bahamas	276.6 (72.7)	55.4 (21.5)	5.3 (1.4)
Florida Keys, USA	222.1 (49.5)	42.3 (18.8)	4.3 (1.8)
Average	**247.3 (64.2)**	**48.5 (18.9)**	**5.1 (1.7)**
Plexaura homomalla forma *homomalla*			
San Blas, Panama	576.0 (199.6)	70.3 (23.0)	8.5 (2.6)
Tague Bay, St. Croix	386.1 (87.5)	47.7 (14.0)	8.6 (2.4)
Chub Cay, Bahamas	458.3 (128.2)	48.5 (18.1)	10.2 (3.2)
Florida Keys, USA	366.4 (113.9)	40.3 (12.9)	9.4 (2.0)
Average	**446.7 (156.0)**	**51.7 (20.6)**	**9.1 (2.7)**
Plexaura homomalla forma *kükenthali*			
Tague Bay, St. Croix (#1)	418.0 (81.9)	46.2 (14.2)	9.6 (2.6)
Tague Bay, St. Croix (#2)	406.7 (103.3)	45.4 (15.4)	9.5 (2.9)
Tague Bay, St. Croix (#3)	368.6 (108.4)	34.3 (12.5)	11.5 (3.8)
Tague Bay, St. Croix (#4)	364.6 (89.4)	35.8 (10.8)	10.7 (2.8)
Carrie Bow Cay, Belize	465.2 (128.2)	62.5 (21.9)	7.9 (2.1)
Average	**404.6 (108.7)**	**44.8 (18.3)**	**9.9 (3.1)**

Morphologic Measurements.—Previous observations (Lasker, 1984) indicated that the comparatively shorter spindles of the middle rind are a valuable diagnostic feature of *Plexaura* A. To quantify this observation, lengths and widths of spindles were measured from *Plexaura kuna* as well as *P. homomalla*, and *P. homomalla* forma *kükenthali*. Sclerites were prepared using whole colony samples as in Bayer (1961). We did not dissect out the middle rind since it was difficult to ensure that certain groups of spindles were not being excluded from this analysis due to their proximity to the adjacent layer. Moreover, spindles were readily distinguishable from other sclerites by their large size, density and shapes of tubercles, and general lack of pigmentation or coloration (i.e., Bayer 1961). Measurements were taken using a dissection microscope fitted with a camera lucida and a digitizing pad calibrated with a stage micrometer. For each colony, 35 spindles were measured. To minimize bias, all spindles in consecutive fields of view were measured. Lengths were measured from tip to tip; widths were taken as maximum thickness excluding tubercle height. Ratios of length to width were also calculated. A nested analysis of variance was performed on natural log transformed lengths and widths and arc tangent transformed length to width ratios.

Genetic Analysis.—RAPDs (randomly amplified polymorphic DNA or arbitrarily-primed [AP]-PCR) use the polymerase chain reaction (PCR) and a single non-specific primer to amplify DNA segments (Williams et al., 1990; Welsh and McClelland, 1990). Polymorphic markers were detected as fragments present in one individual or species, but not in the other. The utility of RAPDs in generating taxonomic specific markers already has been demonstrated in a number of taxa. A variety of 10 bp primers have been used to distinguish between species of dragonflies (Hadrys et al., 1992), irises (Arnold et al., 1991), tomatoes (Klein-Lankhorst et al., 1991), mosquitos (Ballinger-Crabtree et al., 1992), and gorgonians Coffroth and Mulawka (1955) and between clones of bryozoans (Okamura et al., 1993).

We used PCR-generated RAPDs to distinguish *Plexaura kuna* from congeners by identifying species-specific markers for *P. kuna*. We compared RAPD fragment patterns generated from DNA of *P. kuna*, *P. homomalla*, and *P. homomalla* f. *kükenthali*. A total of eight *P. kuna* and 10 *P. homomalla* (both forms) were compared. Samples of *P. kuna* were collected from two sites in the San Blas Islands, Panama, two sites in St. Croix, USVI, two sites in Key Largo, Florida and from Chub Cay and Acklins Is., Bahamas. *P. homomalla* f. *homomalla* samples were collected from the San Blas Islands, Panama and St. Croix, USVI. *P. homomalla moita kükenthali* samples were from St. Croix, USVI. All samples were frozen in liquid nitrogen and kept at −70°C until analyzed.

DNA was extracted from 0.5 cm of tissue according to the methods described in Coffroth et al. (1992). DNA was quantified spectrophotometrically and the concentration adjusted to 5 ng μl^{-1}. Samples were amplified with an arbitrary 10bp primer (Operon Technologies Inc., Alameda, California, USA) in 25 μl with 10 ng of DNA, 1X PCR Buffer (Perkin-Elmer/Cetus), dATP, dCTP, dGTP and dTTP (each at 100 μM), 0.2 μM of primer and 1 unit of Taq polymerase (Perkin-Elmer/Cetus).

Controls that lacked the template DNA were run as a check for outside contamination. Samples were amplified for one cycle of 2.5 min at 94°C, 1 min at 35°C, and 2 min at 72°C and 45 cycles of 1 min at 94°C, 1 min at 35°C, and 2 min at 72°C, followed by a 10 min extension at 72°C. Fragment patterns, generated by electrophoretic molecular weight separation through 1% Synergel (Diversified Biotech) and 0.6% agarose, stained with ethidium bromide and visualized by UV light, were compared among species. A photograph of each gel provided a permanent record.

Reproduction.—Comparisons of the reproductive cycle of *Plexaura* A and *P. homomalla* were made in the San Blas Islands, Panama during the summers of 1983, 1984, 1989, 1992 and 1993. Observations and collections were all made at Korbiski Reef, a small backreef located near the Smithsonian Tropical Research Institute field station (Lasker, 1990 for a map). *P. homomalla* forma *kükenthali* has not been observed in the San Blas (Lasker, personal observation). During 1983–1984 and 1989 collections of marked *Plexaura* A and *P. homomalla* were made at monthly (1983–1984) or 5 day intervals (1989). Samples from 1983–1984 were examined under a dissecting microscope and the number and size of eggs in 10 polyps determined for each specimen. Total gonad volume as well as average gonad diameter were then calculated. Samples from 1989 were embedded in paraffin, sectioned (7 μm) and stained with azocarmine b and aniline blue (Yevich and Barszcz, 1980). Stained slides were examined for number of gonads, state of development and size.

Plexaura A releases eggs starting 15–45 minutes after sunset for 5–6 day periods following the full moons of May or June through August or September (Brazeau and Lasker, 1989). Colonies of *Plexaura* A at Korbiski Reef were monitored for spawning during the months of June–August every year since 1988. During those nights *Plexaura homomalla* colonies were often examined for gamete release. Systematic inspections of *P. homomalla* colonies were made during June and July 1992 and 1993.

Results

Plexaura kuna new species
Figure 1

Description.—Colonies are bushy, slightly flattened, laterally branched up to 1.5 m height (Fig. 1B); terminal branches slightly clavate, up to 3–4 cm long and 2–3 mm in diameter (Fig. 1C). Polyps are weakly armed and lack collarets; anthocodial spindles are less than 10 μm in length with blunt thorns. Surface with a dense layer of leaf clubs with numerous, serrate leaves, and complex tubercles on handle; other leaf clubs with prong-like leaves and blunt thorns on handle (Fig. 2A); flattened or ovoid unilaterally spinose bodies 150–250 μm long with serrate or smooth thorn-like projections (Fig. 2B); spindles up to 200 μm with dense, complex tubercles. Spindles in the middle layer are white (rarely purple), 200–400 μm in length, 4–6 times long as wide, with complex tubercles, a few with blunt thorns (Fig 3A). Axial sheath contains deep reddish, or purple capstans 80–150 μm long (Fig 3B). Sclerites in the basal region of colony are larger (up to 450 μm in length); amorphous bodies with complex tubercles are also numerous. Unlike most gorgonians the axis is relatively brittle and branches preferentialy break off at slight thinnings in diameter that are located immediately above branch points (Lasker, 1984). Air dried colonies are light tan to brown with gaping calyces; colonies preserved in formalin (10% in sea water) and alcohol (75%) are light yellow to light tan.

Type Specimen and Locality.—Holotype, US National Museum 94594; paratype, USNM 94595. Type from Tiantupo Reef, San Blas Islands, Panama (9°33'N, 78°58'W), depth, 1 m.

Known Distribution.—Panama, Bahamas, St. Croix (U.S.V.I.), and Florida Keys USA. All specimens to date have been observed above 15 m depth and *P. kuna* is most common above 10 m.

Etymology.—After the Kuna Indians of San Blas, Panama.

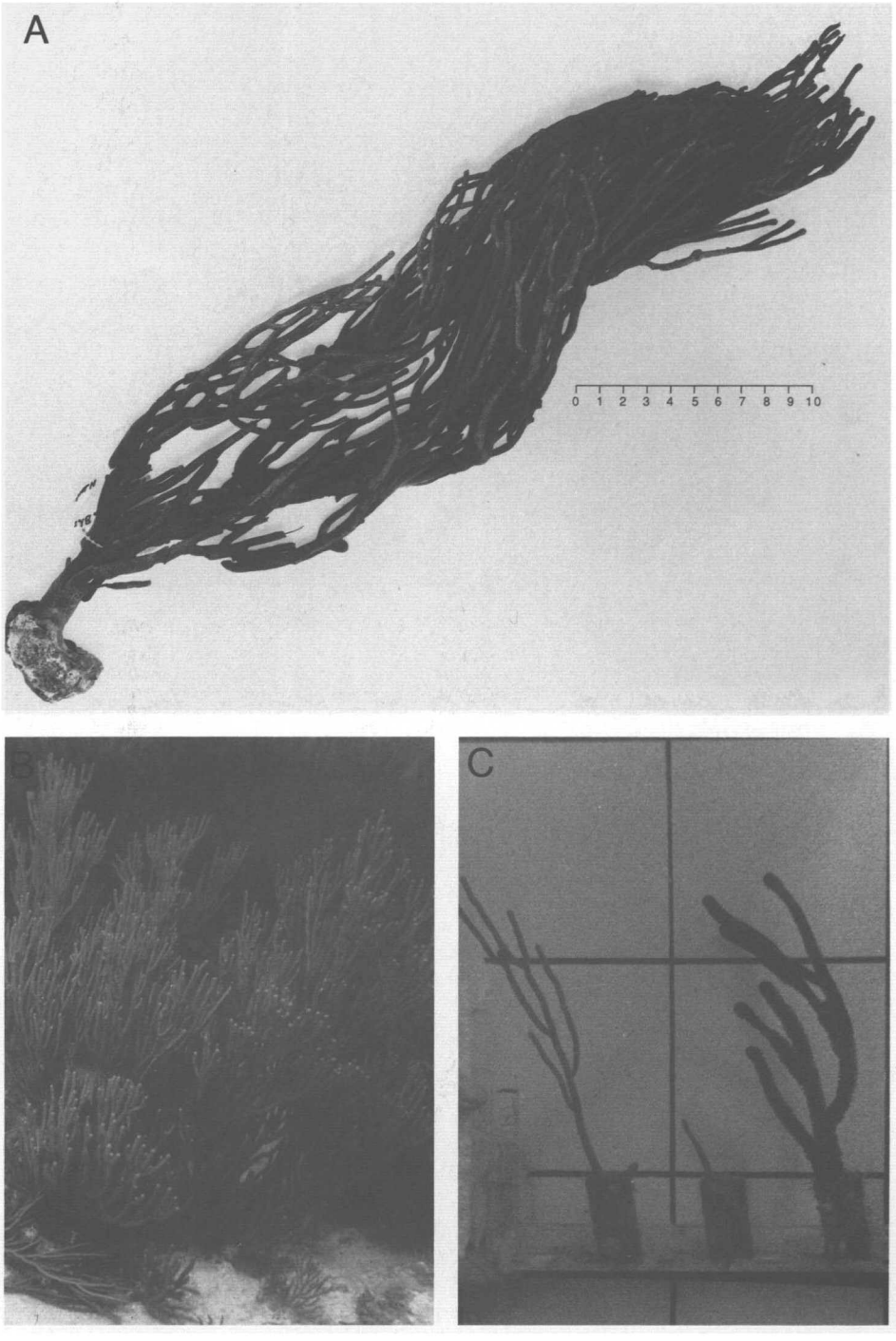

Figure 1. Colonies of *Plexaura kuna*, new species. A, type colony (dried). Scale bar is in cm. B, live *P. kuna* colony at Korbiski Reef, (approximately 80 cm in height); C, closeup of branches of *P. kuna* (light branches) and *Plexaura homomalla* forma *homomalla*. Grid in background of C is 10 cm.

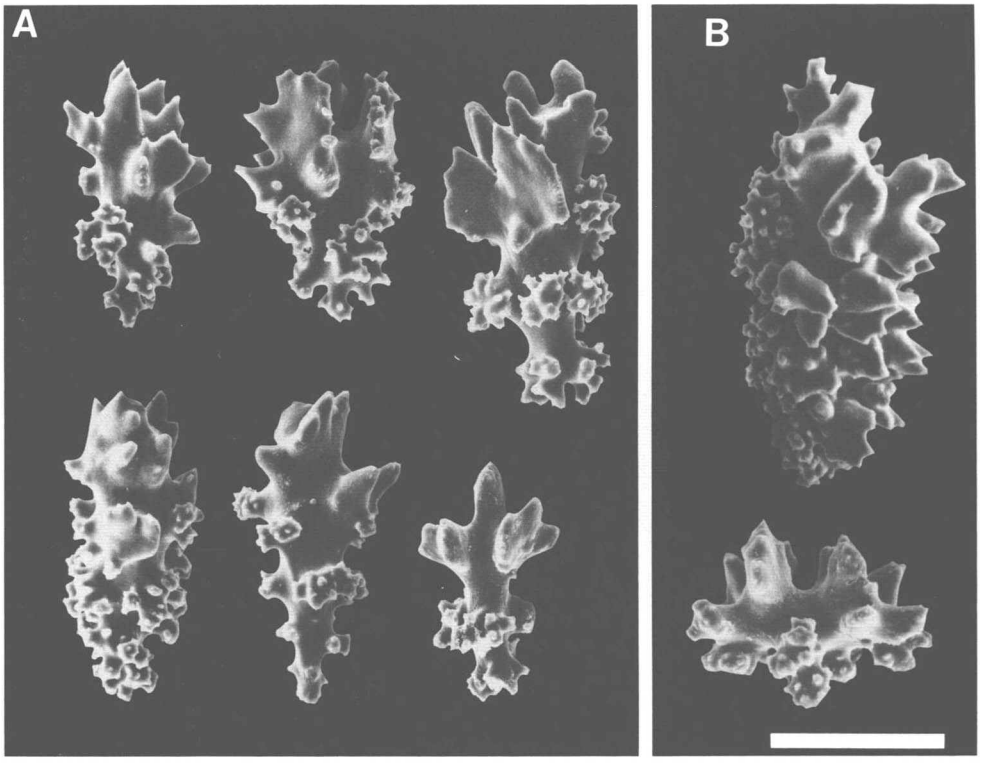

Figure 2. Sclerites from the type colony of *Plexaura kuna*. A, leaf clubs; B, unilaterally spinose bodies of the outer rind. Scale bar = 100 μm.

Remarks.—The smaller, straighter spindles in the cortex, stouter leaf clubs in the rind, the presence of leaf clubs with prong-like processes and the lesser amount of armature of the polyps make *Plexaura kuna* readily distinguishable from either form of *Plexaura homomalla*. *Plexaura homomalla* forma *kükenthali* is the more similar of the two *P. homomalla* morphs, but it has spindles that are longer (>500 μm) and more slender (high L/W ratio) and frequently curved. *Plexaura nina* which also has a grossly similar colony form possesses stronger anthocodial armature as well as a distinct collaret.

In the field *Plexaura kuna* is readily distinguished from the dark brown and laterally branching colonies of *Plexaura homomalla*. *Plexaura flexuosa* are usually more planar, have slightly thicker, more rigid branches and smaller calicular apertures. *P. kuna* colonies are readily distinguished from the typical form of *P. homomalla* by their tan coloration and thinner branches. *P. kuna* is most similar in colony form to *P. homomalla* forma *kükenthali,* but is distinct in having shorter terminal branches and more profuse branching. It also differs from *P. homomalla* forma *kükenthali* by the ease with which its branches can be broken. *P. kuna* branches readily break at branch points sometimes requiring only minor application of force (Lasker, 1984). *P. kuna* branches can reattach to the substrate and in some localities form extensive clones with very high densities of colonies (Lasker, 1984, 1990; Coffroth et al., 1992). Although *P. homomalla* are sometimes clumped in distribution, and sometimes fragment they do so at a dramatically lower rate (H. Lasker, unpubl. data). *P. kuna* colonies are also slimy to the touch

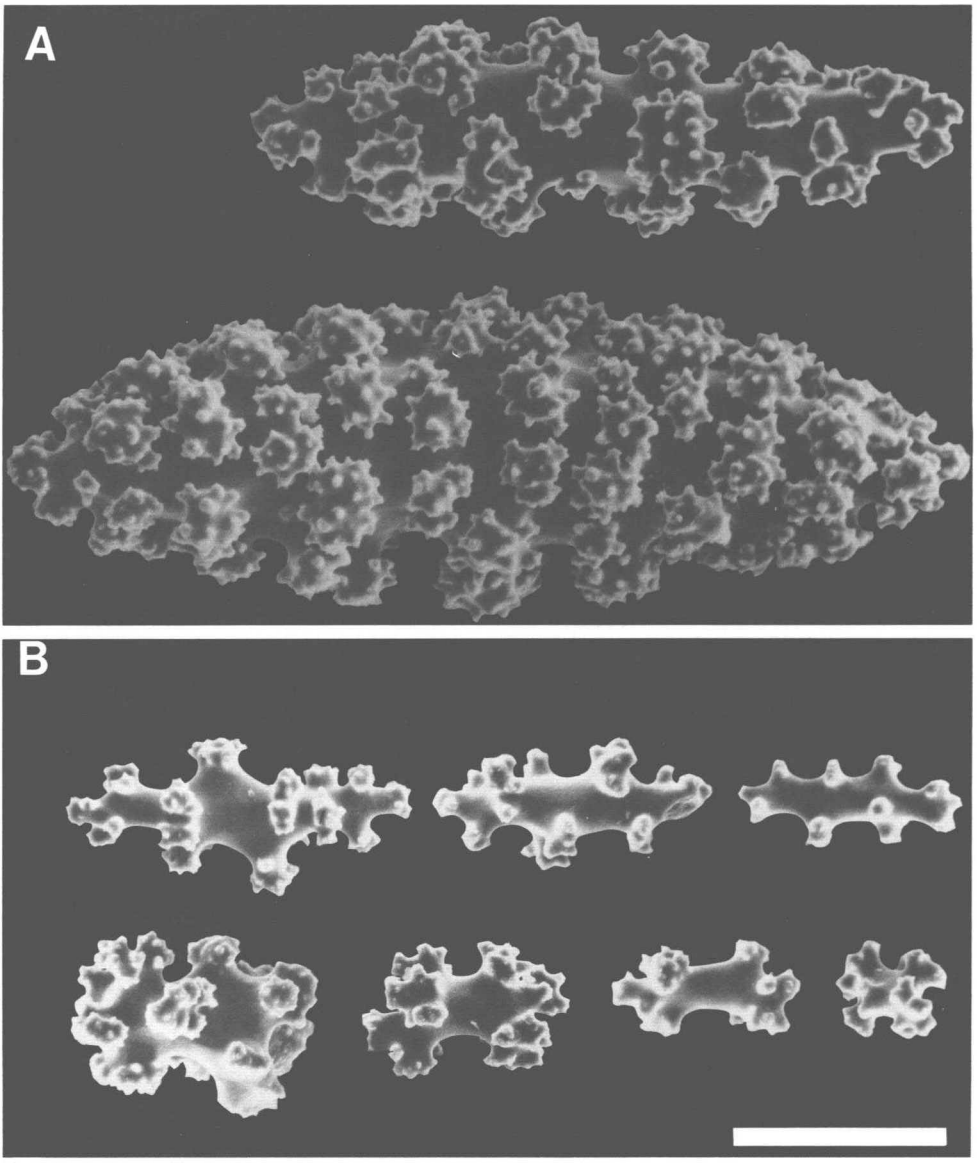

Figure 3. Sclerites from the type colony of *Plexaura kuna*. A, spindles of the middle rind; B, capstans of the axial sheath. Scale bar = 100 μm.

and release more mucus than either form of *P. homomalla* when removed from water.

The only previously described species bearing any similarity to *Plexaura kuna* is *P. ehrenbergi* (Kolliker, 1834). Kükenthal (1924) provides a brief description of the species, but includes no figures. The location of the type is not known to us, and subsequent treatments of *Plexaura* (Staisny, 1935; Bayer, 1961) make no further mention of the species. Like *P. ehrenbergi, P. kuna* has smaller sclerites than other *Plexaura* spp. *P. kuna* cortex spindles are 200–400 μm long. Küken-

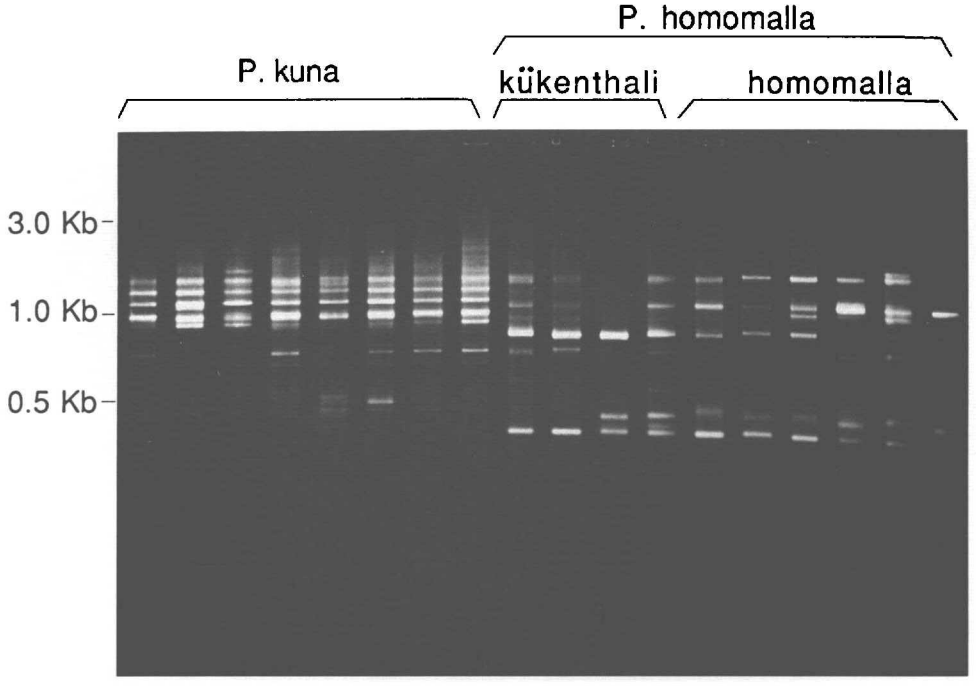

Figure 4. Gorgonian DNA from *Plexaura kuna, P. homomalla* f. *kükenthali* and *Plexaura homomalla* f. *homomalla* amplified with the primer OPS-17. RAPD markers for *P. kuna* are a series of bands between 980 bp and 1,800 bp; With this primer, *P. homomalla* f. *homomalla* and *P. homomalla* f. *kükenthali* are characterized by three bands at 920 bp, 1,160 bp, and 1,720 bp. Molecular weight size markers are indicated on the left.

thal, who only distinguished two layers, noted the presence of spindles of up to 440 μm in *P. ehrenbergi.* There is no mention of the leaf clubs with prong like leaves and thorns on the handle. In the absence of a more detailed description it is impossible to determine whether *P. ehrenbergi* is synonymous with *P. kuna.*

Morphologic Analysis.—A summary of spindle morphology for the three species of *Plexaura* are presented in Table 1. The nested analysis of variance revealed significant variation in all three morphologic parameters both within (Length $F = 38.7$, $P < 0.001$; Width $F = 11.19$, $P < 0.001$; L/W ratio $F = 32.9$, $P < 0.001$) and among species (Length $F = 2216$, $P < 0.001$; Width $F = 1707$, $P < 0.001$; L/W ratio $F = 84.5$, $P < 0.001$). Overall, the spindles in *Plexaura kuna* are much shorter, but are wider, resulting in lower length to width ratios than either *P. homomalla* or *P. homomalla* f. *kükenthali.*

Genetic Analysis.—All *P. kuna,* regardless of site of collection, had a series of bands between 980 bp and 1,800 bp that the other two species lacked. This pattern distinguishes *P. kuna* from *P. homomalla* and *P. homomalla* f. *kükenthali* (Fig. 4). These bands appear to be monomorphic loci within *P. kuna* as they are invariant among these specimens and in other samples from Panama. These bands are never present in either form of *P. homomalla* (Coffroth and Mulawka, 1955). RAPDs of *P. homomalla* and *P. homomalla* f. *kükenthali* colonies were identical when the primer OPS-17 was used. Both morphotypes had diagnostic bands at 920, 1,160 and 1,720 bp.

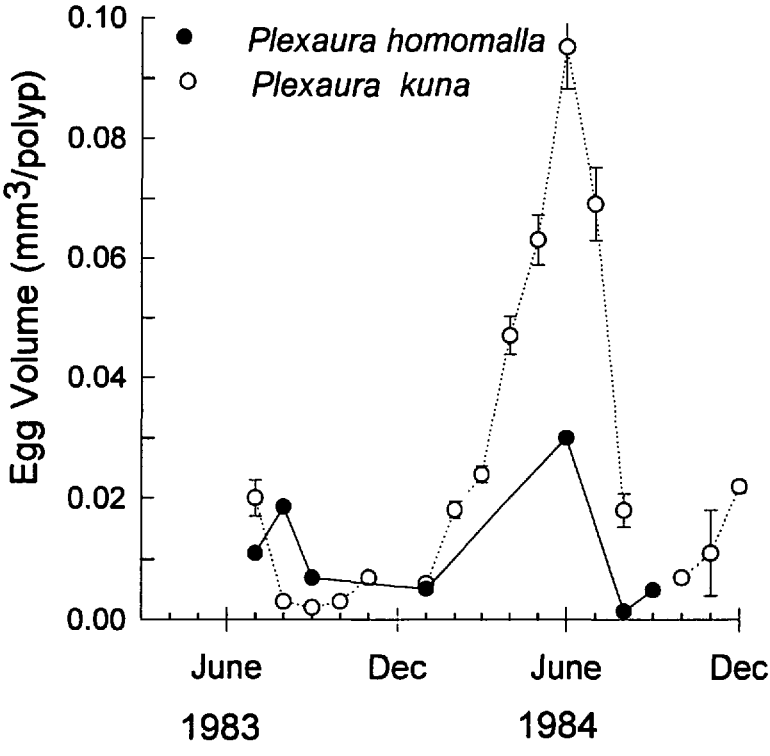

Figure 5. Average total volume of eggs in polyps of *Plexaura kuna* (mean 10 polyps from each of 10 colonies ± standard error) and *Plexaura homomalla* (mean of 10 polyps).

Reproductive Cycle.—The cycle of oogenesis and egg release for *Plexaura kuna* was described by Brazeau and Lasker (1988) and patterns of gametogenesis have been described for both *P. homomalla* and *P. homomalla* forma *kükenthali* (Bayer, 1974; Goldberg and Hamilton, 1974; Behety-Gonzalez and Guardiola, 1979; Martin, 1982). In overall form and time scale the two species are extremely similar. Both species are gonochoric. Brazeau and Lasker (1989) reported an absence of males at their study site, but a small number of male colonies subsequently have been found at that site (Lasker, unpublished data). The low number of males is a function of the small number of clones present on the reef at Korbiski and the coincidental low rate of clonal propagation of the two male clones (Coffroth et al., 1992). Other reefs have 1:1 or male skewed sex ratios (Coffroth and Lasker, unpubl. data).

Eggs have a lengthy development culminating in rapid growth starting several months before spawning. Spermaries are absent most of the year and only become apparent a month prior to spawning. Mature eggs among *P. kuna* colonies are larger than among *P. homomalla* colonies (550 μm vs. 825 μm maximum diameter). Spermatogenesis in *P. kuna* colonies is similar to *P. homomalla* colonies except that mature sperm are present for May and June spawning events instead of the July and August spawning reported for *P. homomalla.* Total gonad volume for a *P. homomalla* female colony as well as average volumes for ten *P. kuna* colonies are present in Figure 5. The single female colony present in the 1983–1984 samples had total gonad volumes lower than the average for *P. kuna.*

P. kuna colonies were surveyed for spawning during 17 summer months be-

tween 1987 and 1993. May spawning was seen only once (in 4 years of observation), whereas spawning during June through September was observed every year observations were made (6 June and 6 July observations, 5 August and 3 September). In contrast, *P. homomalla* spawning was only seen in July and August. In July and August of 1992 and 1993, the months in which the most careful observations were made, *P. homomalla* spawning was observed in late July 1992 and August 1993. Histologic data from 1989 suggest that spawning occurred in August as that was the only month of the summer in which fully mature spermaries were observed. Similarly Bayer (1974) noted that histologic samples from July 20, 1973 contained sperm with tails and samples from August 3 were devoid of mature sperm.

P. kuna spawning events started 3 and in some cases 4 days after the full moon. In contrast, during July 1992 and August 1993, months in which we have careful *P. homomalla* observations, spawning was first observed 9 and 8 days after the full moon respectively. In both of those cases *P. homomalla* spawning overlapped with *P. kuna* on the last and weakest day of *P. kuna* spawning. Bayer's histologic observations (1974) note the presence of sperm with tails 5 days after the full moon suggesting release sometime in the subsequent week. In August 1989 samples had fully mature spermaries 6 days after the full moon, and were devoid of mature spermaries 4 days later.

Discussion

Despite some similarity in colony form between *P. kuna* and *P. homomalla* f. *kükenthali,* there are distinct differences in their sclerites. These differences are clear and of the magnitude used to differentiate other species of gorgonians. However, the correspondence of these distinctions to the biologic species concept has not been examined among any gorgonians. The results of our study suggest that among *Plexaura* spp. the currently described gorgonians are indeed "biologic species." Firstly, the available data indicates that *P. homomalla* forma *kükenthali* has the same reproductive pattern as the typical form of *P. homomalla* (Behety-Gonzalez and Guardiola, 1979; Martin, 1982). In contrast gametogenesis in *P. kuna* follows somewhat different timing than *P. homomalla* and more importantly there is relatively little overlap in spawning of the two species. In Panama the vast majority of *P. kuna* gametes are released on nights that *P. homomalla* does not spawn. The completeness of this reproductive isolation is supported by the RAPD data, which shows that *P. kuna* specimens from different localities throughout the Caribbean share a set of alleles that are totally absent in *P. homomalla* and *P. homomalla* forma *kükenthali. P. homomalla* and *P. homomalla* forma *kükenthali,* which have similar patterns of gametogenesis, could not be differentiated genetically using the PCR primer OPS 17. This latter finding is not a demonstration of panmixis between the two groups but it is consistent with such a pattern. This suggests that Bayer's assignment of *P. homomalla* forma *kuekenthalialla* as a form rather than as a separate species correctly characterizes its taxonomic status.

Among gorgonians (Harvell et al., 1993; West et al., 1993; Brazeau and Harvell, 1994) as well as among other reef taxa (bryozoa—Cheetham and Jackson 1990; scleractinians—Knowlton et al., 1992; Stobart and Benzie, 1994) there is a growing awareness that there is a strong genetic basis to much of the variability observed in nature, and that in at least some cases species that have been described as highly plastic are in fact complexes of sibling species. As Knowlton and Jackson (1994) note, the implications of such differentiation are great and the com-

munity ecology and evolution of tropical marine taxa may indeed be more complex than hitherto believed.

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